

SYSTEMATICS AND BIOGEOGRAPHY OF THE
NEW ENGLAND COTTONTAIL,
SYLVILAGUS TRANSITIONALIS (BANGS, 1895),
WITH THE DESCRIPTION OF A NEW SPECIES
FROM THE APPALACHIAN MOUNTAINS

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Abstract.—Multivariate statistical analyses of 19 cranial and toothrow measurements of 274 adult cottontails, hitherto referred to as *Sylvilagus transitionalis*, were undertaken. Our results provide clear evidence of two morphometrically distinct taxa within what has conventionally been regarded as a single species, *S. transitionalis*, and thus support previous investigations which had revealed two discrete karyotypes ($2N = 46$; $2N = 52$). We consider the congruence in data sets to support the recognition of two sibling species in *S. transitionalis*. As here defined, the New England cottontail, *S. transitionalis* ($2N = 52$), is restricted to boreal habitat in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island and New York as far west as the Hudson River. The new Appalachian cottontail species, *Sylvilagus obscurus*, is generally an inhabitant of higher elevations and is restricted to the Appalachian Mountains and their associated mountain balds from the Hudson River through New York, Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia and Alabama. The two species are phenotypically very similar but subtle differences in cranial shape, particularly in the anterior and medial portions of the skull, allow for their delineation. Diagnostic cranial ratios, indicated by multivariate procedures, in conjunction with the results from discriminant function analysis, provide a reliable and practical means of species identification in the absence of chromosomal data. In addition we speculate on the possible biogeographic processes in the New York area that may have contributed to the evolutionary divergence of these taxa during the Wisconsinan glaciation.

As currently understood, the New England cottontail, *Sylvilagus transitionalis*, is primarily an inhabitant of dense woodland and boreal environments (Chapman & Paradiso 1972, Chapman 1975, Chapman et al. 1982, Chapman & Ceballos 1990). The species is reported to range from southeastern New England south, along the Appalachians, to Alabama (Hall 1981, Chapman & Stauffer 1981). Within this region it has a mosaic distribution that is thought to reflect, in part, gradual climatic change since

the last glaciation and the concomitant re-invasion of lowland areas by the more ubiquitous eastern cottontail, *S. floridanus*. These factors prompted Chapman & Stauffer (1981) to propose that *S. transitionalis* exists only as a refugial relict within the southern parts of its range.

More recently, however, the taxonomic status of *S. transitionalis* has been questioned by the finding of two distinct chromosomal races within its presumed geographic range; a northern race characterized

by $2N = 52$ (Holden & Eabry 1970, Wilson 1981, Ruedas et al. 1989) and a southern karyotype with $2N = 46$ (Robinson et al. 1983, Ruedas et al. 1989). Based on this evidence Ruedas et al. (1989) concluded that the two chromosomal races occur parapatrically such that the northern karyotype extends roughly from the Wisconsinan terminal moraine northwards and the southern race from the same point southwards (Ruedas et al. 1989). Since there is no evidence of hybridization between the two karyotypes (Ruedas et al. 1989), it is probable that the chromosomal races represent two sibling species in what has traditionally been regarded as *S. transitionalis*.

The presence of two genetically distinct sibling species in *S. transitionalis* would profoundly affect the interpretation of many previous studies, especially those directed towards the conservation of a species which is considered vulnerable by virtue of its restricted distribution (Chapman & Stauffer 1981, Feldhamer et al. 1984, Webster et al. 1985, Mount 1986, Chapman & Ceballos 1990). Therefore, the aims of this study were: (1) to determine whether other parameters would similarly reflect evidence of a discontinuity following intraspecific analysis and, in so doing, further delineate the geographic distributions of the two reported karyotypes, (2) to attempt to identify the possible underlying factors that may have led to the present biogeography of these two species. A morphometric appraisal of a suite of cranial and dental measurements was undertaken on museum specimens whose collection localities span the entire range of what has been conventionally regarded as *S. transitionalis* and which includes the probable zone of parapatry suggested by the cytogenetic data (Holden & Eabry 1970, Robinson et al. 1983, Ruedas et al. 1989).

Methods

Where possible, 28 skull and tooththrow measurements (Robinson & Dippenaar

1987) were recorded from each specimen from a preliminary data set ($n = 283$). All measurements were taken with dial calipers to the nearest 0.1 mm. Multivariate statistical analyses were performed using selected sub-routines of BIOSTAT II (Pimentel & Smith 1986) and the Numerical Taxonomy System (NTSYS-pc; Rohlf 1986). The statistical procedures used in this investigation have been reported elsewhere (Robinson & Dippenaar 1983) and are similar to those used by Genoways (1973), Swanepoel & Schlitter (1978) and Dippenaar & Rautenbach (1986).

Those measurements found to have low repeatability (zygomatic arch length, posterior cranial height, interauditory breadth) were excluded from analysis. Furthermore, in order to remove excessive redundancy due to high correlations between measurements, a correlation matrix was calculated for all pairs of measurements derived from a subset of 30 specimens drawn from geographically contiguous populations in Wyndham and Tolland Counties, Connecticut, and clustered by the unweighted pair group method using arithmetic averages (UPGMA). Four length measurements (total length of skull, basal cranial length, maximum mandibular length, mandibular tooththrow length) were highly correlated ($r \geq 0.84$); total length of skull was consequently retained as representative of these length measurements. Likewise, the relatively high correlations ($r \geq 0.71$) between palate vacuity length: palate incisor length; maxillary premolar length: maxillary premolar-molar length; palatal breadth: bizygomatic breadth, together with the numbers of specimens characterized by missing values for several of these measurements, led to further character exclusion and the retention of the second measurement in each case. As a result, a suite of 19 cranial and tooththrow measurements from 274 adult specimens was finally retained for comprehensive analysis. These measurements included, total length of skull, muzzle length,

Table 1.—Delimitation of geographic populations (OTUs) for analysis in a 19-character Principal Component Analysis. OTUs represent grouped localities where these are geographically contiguous or, in instances involving more isolated populations, single localities even where these are represented by single specimens. The numbers representing each OTU's constituent populations correspond to those contained in the Gazetteer.

OTU no.	Constituent population(s)	OTU no.	Constituent population(s)	OTU no.	Constituent population(s)
1	1–2	15	73–74, 86	29	117
2	3–4	16	75–77, 79–80	30	118–119
3	91, 23–24	17	78, 81–84	31	116
4	5–6	18	87	32	120–121
5	7–8	19	88–89	33	122
6	25–26	20	90	34	123
7	9–12	21	92	35	124
8	13–18	22	93	36	126–127
9	19–22	23	94	37	125
10	27	24	95	38	128
11	28–29	25	96	39	131–132
12	30–32	26	115	40	129–130
13	34–43	27	97–109		
14	33, 44–72, 85	28	110–114		

frontal length, parietal length, posterior muzzle breadth, anterior frontal breadth, posterior frontal breadth, palate vacuity length, hard palate length, mesopterygoid space, maxillary premolar-molar length, principal I¹ breadth, palatal breadth, maximum cranial breadth, bulla breadth, maximum mandibular height, mandibular body breadth, I₁ breadth and mandibular premolar-molar length (see Robinson & Dippenaar 1987, for definition of measurements).

To reduce the effects of age variation, statistical analyses were conducted only on measurement of adults. Age was determined by using the fusion of the suture between the exoccipital and supraoccipital bones (Hoffmeister & Zimmerman 1967). Specimens of adults sorted by state of collection, were subsequently tested for secondary sexual dimorphism using a single classification analysis of variance. Only muzzle length and mesopterygoid space showed significant differences between the sexes ($P < 0.05$) thereby confirming other studies that span several lagomorph genera, all of which indicate that almost all disparities in measurement between the sexes are

slight and statistically non-significant (Chapman 1971; Chapman & Morgan 1973; Taylor et al. 1977; Baker et al. 1978; Yates et al. 1979; Diersing & Wilson 1980; Robinson & Dippenaar 1983, 1987). The sexes were subsequently pooled and the combined data set subjected to further analysis.

Following preliminary analyses to ensure the homogeneity of individual and pooled samples, multivariate statistical analyses were performed, where possible, on arithmetic mean values for each measurement obtained from grouped localities (geographically contiguous samples). However, geographically isolated populations were treated independently, even when represented by single specimens. Using this approach, forty geographic populations (OTUs) were identified (Table 1) and analyzed by cluster and principal component analysis (PCA). Phenograms were generated from both the Pearson's product-moment correlation and average taxonomic distance matrices, and cophenetic correlation coefficients were calculated in order to assess the goodness of fit between phenograms (and PCA scattergrams) and the original standardized matrices. The PCA was based on correlation

coefficients among characters. Two-dimensional projections of the samples on the first three components were made, and the correlation between the characters and these components as well as the percentage variation accounted for by them were computed. These analyses formed the basis of our taxonomic conclusions.

A discriminant function analysis was employed to assess the integrity of a priori designated groups. This was done by contrasting specimens derived from localities along the Appalachian mountains (high elevation areas; Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia and Alabama—referred to as “Appalachian” = *Sylvilagus* sp. nov.) with those from predominantly low elevation regions (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, and New York—referred to as “non-Appalachian” = *S. transitionalis*). This grouping, loosely suggested by the cytogenetic data (Robinson et al. 1983, Ruedas et al. 1989), was supported by the PCA (Fig. 1). Furthermore, since the discriminant function analysis requires a full data set for each specimen classified, OTUs with missing values were excluded from the analysis resulting in a sample size of 216, of which 138 were a priori classified as “non-Appalachian” and 78 as “Appalachian.”

To assist with species identification, diagnostic ratios between selected measurements were calculated. Likewise, the standardized canonical vectors generated by the discriminant function analysis are presented as an aid in species identification. While cytogenetic data provide for the unequivocal identification of “Appalachian” (*Sylvilagus* sp. nov.) or “non-Appalachian” (*S. transitionalis*) specimens, these are not always available, making the correct classification, particularly of museum specimens, problematic. However, by recording the 19 cranial and dental measurements on which the present analysis is based, animals lacking cytogenetic data, or museum specimens

of dubious provenance, can be correctly classified with a high degree of accuracy. This can be done by: (1) subtracting the total sample mean of each measurement from the corresponding measurement of the unknown, (2) multiplying these derived values by the corresponding canonical vectors, (3) summing them for all 19 measurements and subsequently determining the group with which the unknown has the greatest affinity (Robinson & Dippenaar 1983).

Systematics

Both distance and correlation phenograms were computed from matrices based on standardized values. Although little structure was evident in the distance phenogram, clear separation of the OTUs originating from the Appalachian Mountains (*Sylvilagus* sp. nov.; OTU 21–40) from those in the “non-Appalachians” (*S. transitionalis*; OTU 1–20) was evident in the correlation phenogram (Fig. 2; cophenetic correlation coefficient 0.679). Cluster A comprised all those specimens initially defined as having been derived from “Appalachian” localities but excludes OTU 24 (Centre Co., Pennsylvania), which is represented by a single specimen (PM 3342) incorrectly clustered within the “non-Appalachian” assemblage B. Other misplaced OTUs, all “non-Appalachian” in designation, are OTU 4 (Sullivan Co., New Hampshire, USNM 508323 and 507723), OTU 19 (Westchester Co., New York, AM 5728 and Westchester Co., New York, USNM 188140 and 189138) and OTU 20 (Sullivan Co., New York, AM 69379). The two major clusters A and B are well differentiated from each other, joining at an average correlation of -0.15 .

The amount of phenetic variation represented by the first two principal components was 50.6% (cophenetic correlation 0.856) while the third component contributed an additional 10.7% accounting, accumulatively, for 61.3% of the total phe-

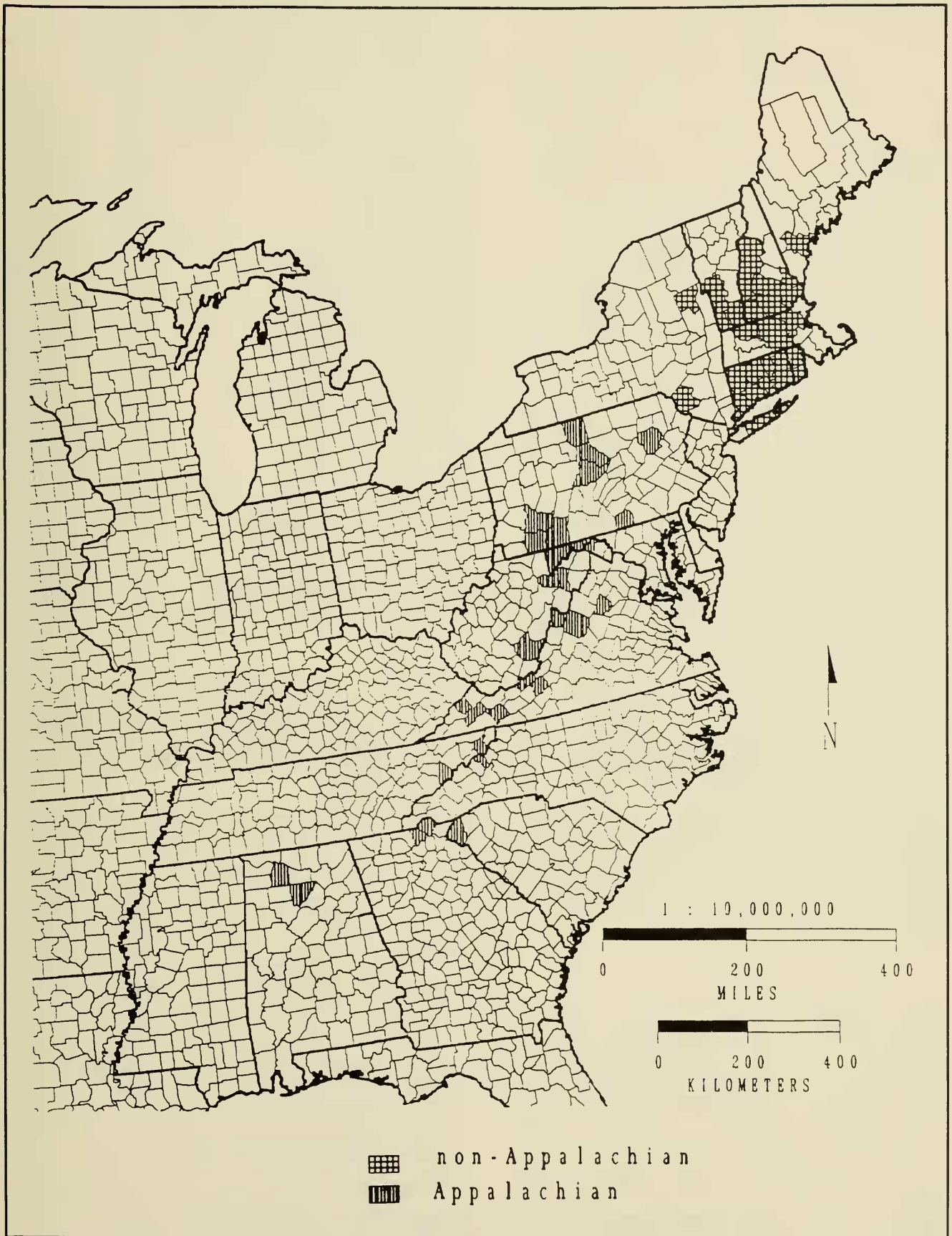


Fig. 1. Counties from which 274 specimens used in PCA and discriminant function analysis were collected, showing "non-Appalachian" and "Appalachian" a priori classification.

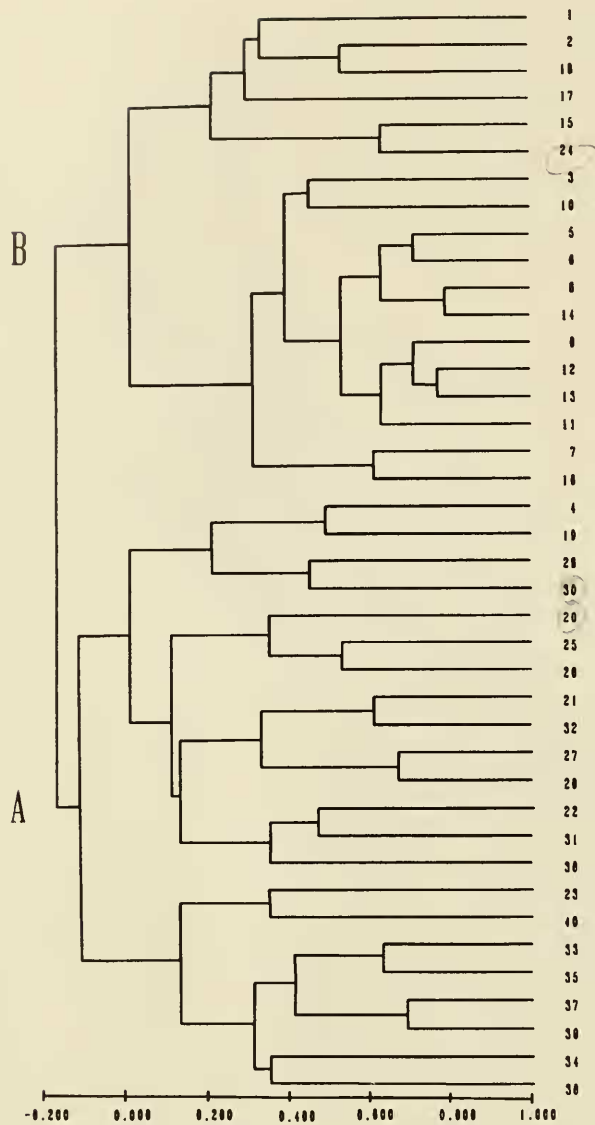


Fig. 2. Correlation phenogram with OTUs clustered by the unweighted pair-group method using arithmetic averages. OTUs 1–20 = *S. transitionalis*; OTU 21–40 = *S. obscurus*. See Table 1 for each OTU's constituent population(s).

netic variation (Table 2, Fig. 3). The first component is largely influenced by size as indicated by the high positive loadings for most measurements, including total length of the skull, maxillary premolar-molar length and mandibular premolar length. The second component is more complex, highlighting shape differences principally in the anterior mid-portion of the skull. This is reflected in the relatively high positive loadings for parietal length, palate vacuity length and mandibular body breadth, and high

Table 2.—Factor matrix from a 19-character principal component analysis based on values for each of 40 localities throughout the geographic ranges of *S. transitionalis* and *S. obscurus*.

Measurement	Factor I	Factor II
Total length of skull	0.894	-0.152
Muzzle length	0.632	-0.028
Frontal length	0.334	0.027
Parietal length	0.019	0.555
Post. muzzle breadth	0.622	-0.419
Ant. frontal breadth	0.162	0.147
Post. frontal breadth	-0.240	-0.563
Palate vacuity length	0.505	0.550
Hard palate length	0.460	-0.432
Mesopterygoid space	0.727	0.046
Max. premolar-molar length	0.873	0.158
Principal I' breadth	0.450	-0.583
Palatal breadth	0.788	0.272
Max. cranial breadth	0.714	0.138
Bulla breadth	0.628	-0.115
Max. mandibular height	0.550	-0.683
Mandibular body breadth	0.647	0.431
I ₁ breadth	0.616	0.020
Mand. premolar-molar length	0.887	0.103

negative values for posterior frontal breadth, posterior muzzle breadth, hard palate length, upper principal incisor breadth and mandibular height.

Examination of principal component plots (I:II; I:III; II:III) revealed that while there is little meaningful separation of OTUs along either component I or III, discrimination reflecting subtle shape differences between OTUs is evident on the second axis. With respect to the ordination along the second component (Fig. 3) a pattern similar to that shown in the correlation phenogram was found. Specifically, the "non-Appalachian" OTUs 1–20 are, almost exclusively, clustered in the bottom half of the two dimensional space and well separated from those derived from geographic populations designated as "Appalachian" (OTUs 21–40) which, with the exception of OTUs 26 and 29 (each represented by single specimens) are more loosely grouped in the upper half of the second component scale.

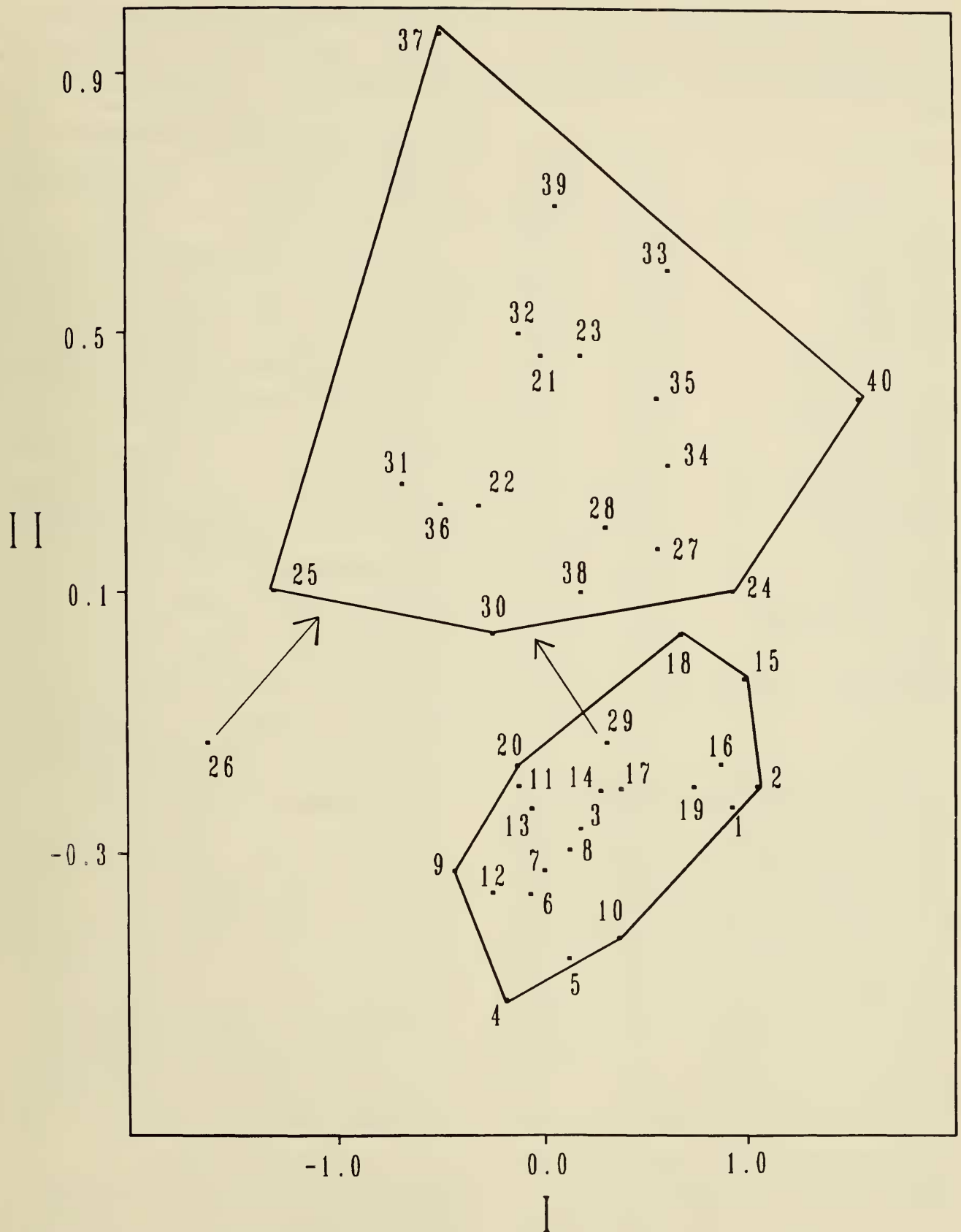


Fig. 3. Scattergram of components I and II from a principal component analysis based largely on sample means; OTUs 1-20 = *S. transitionalis*; OTU 21-40 = *S. obscurus*. See Table 1 for each OTU's constituent population(s).

Table 3.—Standardized canonical vectors for the 19 cranial and toothrow measurements resulting from a two-group discriminant function analysis of a priori grouped specimens of *S. obscurus* and *S. transitionalis* OTUs.

Measurement	Total sample means (mm)	Standardized canonical vectors
Total length of skull	70.964	-0.045
Muzzle length	25.991	0.157
Frontal length	33.244	-0.034
Parietal length	15.362	-0.114
Post. muzzle breadth	14.174	0.660
Ant. frontal breadth	15.307	-0.849
Post. frontal breadth	13.876	0.422
Palate vacuity length	17.406	-0.313
Hard palate length	6.040	1.026
Mesopterygoid space	6.866	0.390
Max. premolar-molar length	14.329	0.496
Principal I' breadth	2.695	4.785
Palatal breadth	20.519	-0.748
Max. cranial breadth	26.533	-0.482
Bulla breadth	8.393	0.074
Max. mandibular height	33.389	0.441
Mandibular body breadth	4.475	-0.511
I ₁ breadth	2.593	-2.148
Mand. premolar-molar length	14.241	-0.264

Discriminant function analysis of 19 cranial and toothrow measurements from specimens characterized by full data sets was used to distinguish between the a priori groups of specimens categorized as “non-Appalachian” ($n = 138$) and “Appalachian” ($n = 78$). Standardized canonical vectors from this analysis are presented in Table 3. Of the 216 specimens used in the discriminant analysis, 210 (97.2%) were classified correctly and six (2.8%) incorrectly. The two groups were delineated by $DS_{0.5} = -0.50$ and with the exception of the OTUs listed below, the discriminant scores of the “non-Appalachian” group ranged from 3.78 to -0.34 (centroid = 1.29) whereas the scores of the “Appalachian” group ranged from -0.64 to -5.38 (centroid = -2.29). Of the six misclassified specimens, two “Appalachian” OTUs had discriminant scores only slightly larger than the $DS_{0.5}$ value (0.26; 0.16), two “non-Appalachian” specimens

had discriminant scores marginally below the $DS_{0.5}$ value (-0.76 in both instances). More problematic was the aberrant classification of two “non-Appalachian” OTUs derived, respectively, from Cumberland Co., Maine (USNM 507686; discriminant score -1.71) and Sullivan Co., New York (AM 69379; discriminant score -1.48).

Two reasons, not necessarily mutually exclusive, may be advanced for the misclassification of the a priori grouped specimens. First, the anomalous classification may reflect possible measurement errors. Support for this hypothesis is that with one exception (Sullivan Co., AM 69379), the misclassified specimens formed part of a series, the constituents of which were derived from a single locality or, alternatively, contiguous localities in the same county. Second, the misclassification may reflect errors in our a priori assignment of specimens as “Appalachian” and “non-Appalachian” in the discriminant function analysis. There may be distributional overlap between the two forms such that the “Appalachian” karyotype ($2N = 46$) also exists as insular relicts in isolated montane habitat within the low-lying areas that accommodate the $2N = 52$ form.

Our analyses support the identification of two phenetic entities within what conventionally has been referred to as *S. transitionalis*. We believe that specimens to the north and northeast of the Hudson River form a discrete species which, given the existing cytogenetic data, is characterized by a $2N = 52$ karyotype (Holden & Eabry 1970, Wilson 1981, Ruedas et al. 1989). We refer these specimens to *S. transitionalis*, with the type locality being Liberty Hill, New London Co., Connecticut (Bangs 1895). This includes localities characterized by both relatively high montane habitat (Vermont and New Hampshire) and low-elevation terrain (Maine, Connecticut, Massachusetts, Rhode Island). Specimens derived from localities west and south of the Hudson River, at points along the reaches of the Appalachian mountain chain as far south as Georgia and

Table 4.—Skull measurements of *S. transitionalis* and *S. obscurus*. *SD* = standard deviation, *CV* = coefficient of variation and *n* = sample size.

Measurement	Mean (mm)	<i>SD</i>	<i>CV</i>	<i>n</i>	Range (mm)
A: <i>S. transitionalis</i>					
Total length of skull	70.95	1.99	2.81	174	75.90–65.80
Muzzle length	26.10	1.41	5.39	178	30.22–21.66
Frontal length	33.21	1.57	4.72	175	37.01–29.49
Parietal length	15.42	0.79	5.21	175	17.63–12.28
Post. muzzle breadth	14.32	0.74	5.16	178	16.46–12.63
Ant. frontal breadth	14.79	0.85	5.72	176	17.02–12.78
Post. frontal breadth	13.97	0.82	5.84	174	16.43–11.86
Palate vacuity length	17.27	0.77	4.46	178	19.18–15.40
Hard palate length	6.17	0.41	6.69	179	7.15–5.12
Mesopterygoid space	6.82	0.48	7.04	179	8.01–5.74
Max. premolar-molar length	14.32	0.60	4.16	179	16.02–12.90
Principal I ¹ breadth	2.74	0.13	4.74	177	3.06–2.34
Palatal breadth	20.38	0.63	3.10	179	21.88–18.97
Max. cranial breadth	26.47	0.66	2.51	165	29.02–24.84
Bulla breadth	8.35	0.26	3.13	167	9.31–7.68
Max. mandibular height	33.63	1.13	3.36	168	36.26–30.66
Mandibular body breadth	4.46	0.21	4.77	173	5.04–3.84
I ₁ breadth	2.59	0.13	4.97	172	2.92–2.20
Mand. premolar–molar length	14.22	0.54	3.82	171	15.64–12.84
B: <i>S. obscurus</i> :					
Total length of skull	70.82	2.05	2.89	91	75.16–65.50
Muzzle length	25.81	1.52	5.88	95	30.68–21.02
Frontal length	33.32	1.57	4.71	93	37.04–28.86
Parietal length	15.53	0.97	6.24	90	18.44–13.42
Post. muzzle breadth	13.95	0.88	6.30	95	15.92–11.89
Ant. frontal breadth	16.22	1.15	7.11	92	19.12–13.63
Post. frontal breadth	13.71	0.86	6.24	94	15.56–12.22
Palate vacuity length	17.65	0.78	4.41	93	19.58–15.76
Hard palate length	5.76	0.38	6.62	94	6.76–5.04
Mesopterygoid space	6.96	0.42	6.00	95	8.37–6.14
Max. premolar-molar length	14.33	0.56	3.94	95	15.95–13.11
Principal I ¹ breadth	2.62	0.14	5.40	95	2.89–2.26
Palatal breadth	20.76	0.66	3.16	95	22.01–18.87
Max. cranial breadth	26.70	0.74	2.76	92	28.72–24.81
Bulla breadth	8.41	0.31	3.73	93	8.99–7.68
Max. mandibular height	32.95	1.20	3.63	92	35.79–30.09
Mandibular body breadth	4.50	0.21	4.63	95	5.21–4.06
I ₁ breadth	2.61	0.11	4.36	95	2.94–2.38
Mand. premolar–molar length	14.26	0.51	3.59	94	15.87–13.23

Alabama are phenetically distinct from *S. transitionalis* and, although cytogenetic data from Pennsylvania, North Carolina and further south are not available, are all considered likely to possess the $2N = 46$ karyotype (Robinson et al. 1983, Ruedas et al. 1989). We refer these high-elevation specimens to the Appalachian cottontail.

There is considerable overlap in the observed ranges of all 19 characters used in this study (Table 4) indicating the difficulties associated with discriminating between the two species without resorting to cytogenetic analyses. However, unlike the absolute values, proportionate differences of diagnostic value are evident when ratios are

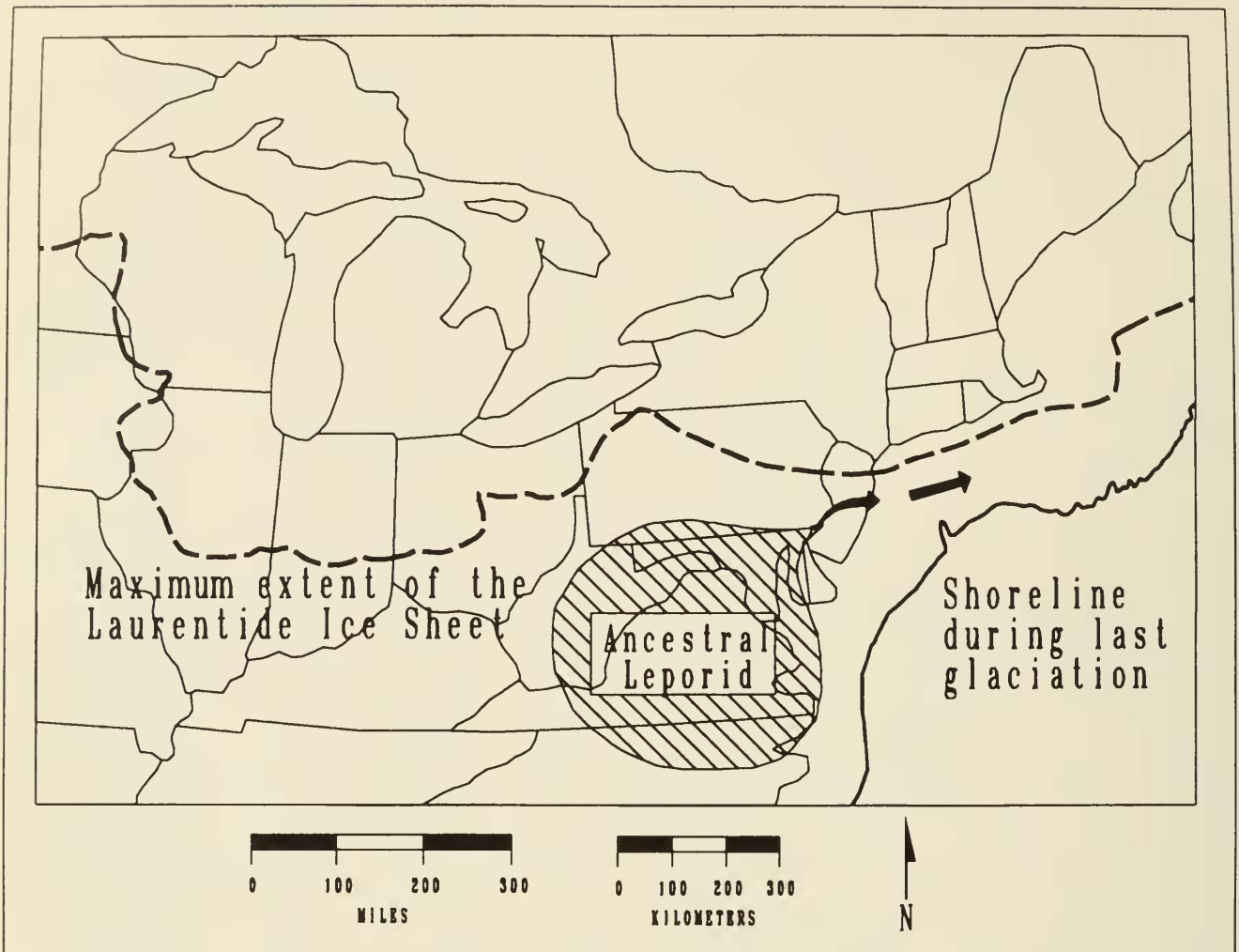


Fig. 4. Hypothesized invasion of the ancestral *transitionalis/obscurus* leporid along the eastern edge (dotted line) of the Laurentide ice sheet. Map details from Knebel (1981) and Morgan (1987).

calculated by contrasting selected measurements with high positive loadings on component II against those with high negative loadings (Table 2). In the Appalachian cottontail the skull is proportionately shorter anteriorly, and medially narrower, than in *S. transitionalis*. Two of the ratios characterized by no overlap in mean \pm one standard deviation (I^1 breadth: anterior frontal breadth, and hard palate length: anterior frontal breadth) are particularly useful in taxon delineation (Table 5).

Biogeography

Our proposal that the Hudson River delineates the geographic distributions of the two species does not imply that the waterway is now completely effective in restrict-

ing movement between karyotypes, although it undoubtedly has been in the evolutionary past (Teller 1987). In this regard, included in our analysis are several specimens from New York State localities marginally east and west of the Hudson River (Sing Sing and Hastings, Westchester Co. (east) represented by OTU 19 in the PCA; Monticello, Sullivan Co. (west) represented by OTU 20 in the PCA) considered by us to be low elevation "non-Appalachian" specimens (*S. transitionalis*) but which, interestingly, behave somewhat inconsistently in the two types of analysis used in this investigation. While hybridization between the species cannot be excluded, given the magnitude of the chromosomal differences that distinguish the respective genomes (Ruedas et al. 1989), it is unlikely.

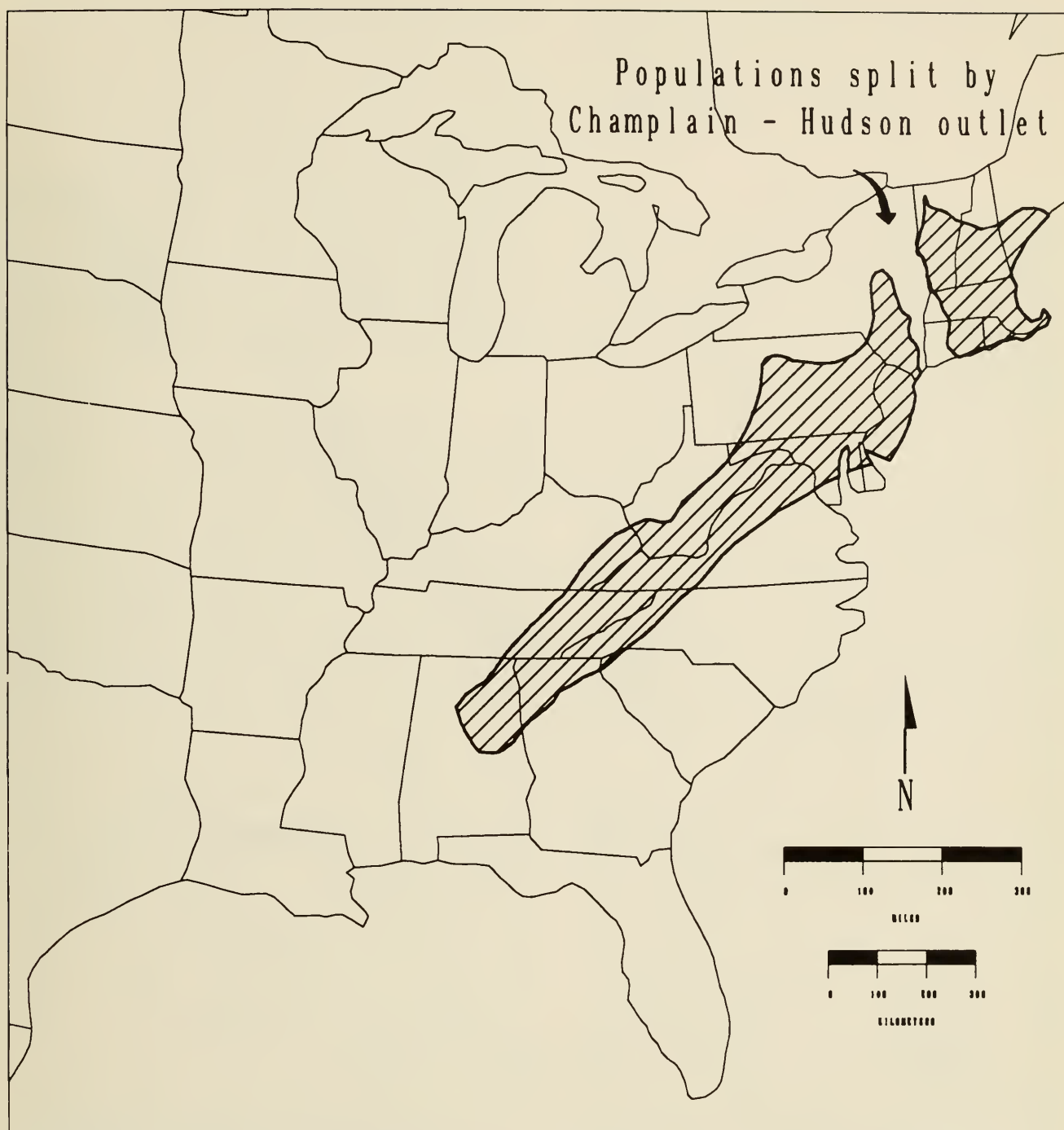


Fig. 5. Proposed geographic isolation of the ancestral *transitionalis/obscurus* populations by the eastward shift in the Champlain-Hudson outflow. Map details from Teller (1987) and Hall (1981).

Although simple fusion of heterozygotes often segregate in a balanced fashion, the paracentric inversion difference involving one of the fusion elements (chromosome 4 of Ruedas et al. 1989) is likely to result in more complex meiotic configurations and impaired fertility of the heterozygotes (Robinson et al. 1991). However, irrespective of these considerations, future studies directed

at refining the contact zones between the species should involve extensive sampling along the borders of the Hudson River and Lake Champlain.

We believe that a series of events similar to those illustrated in Figs. 4–6, occurred over the last 18,000 to 10,000 yr and resulted in the evolution of these two sibling species. We hypothesize that the ancestral

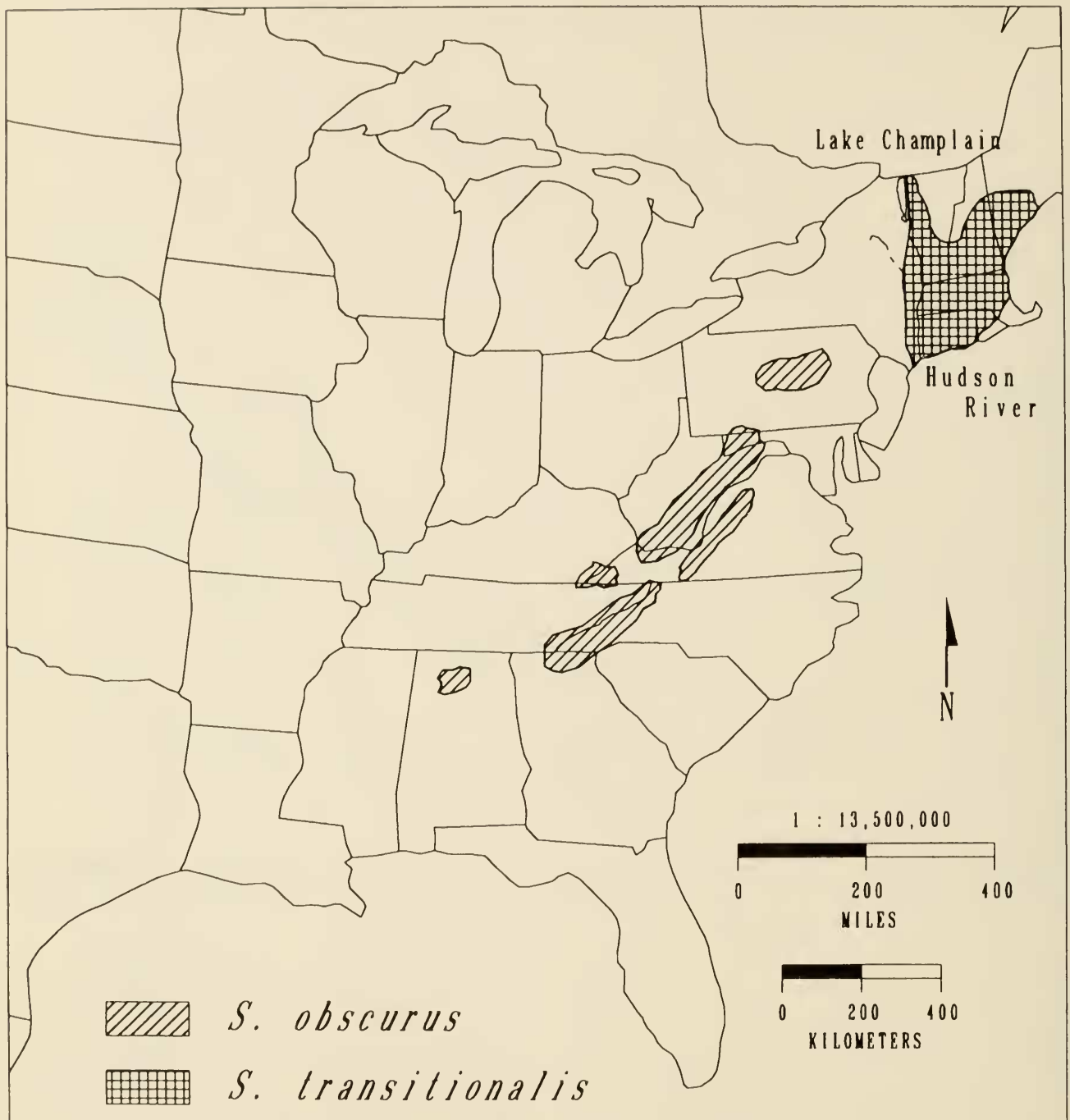


Fig. 6. Current distribution of *S. transitionalis* and *S. obscurus*. Distribution map based on this study and data collected by Chapman and Stauffer (1981).

leporid invaded northwards along the Laurentide ice sheet about 18,000 yr B.P. (Fig. 4; Morgan 1987). As the Laurentide ice sheet receded 10,000–12,000 yr B.P., and the outflow shifted eastward from the Champlain-Hudson Valley System (Fig. 5; Teller 1987), this split the ancestral leporid group into two populations which later led to the evolution of the extant *S. transitionalis* and the species described herein.

In essence, the conclusions drawn from our morphometric analysis concur with those of Ruedas et al. (1989). These authors propose that the two karyotypes occur parapatrically, with the northern karyotype ($2N = 52$) extending from the Wisconsinan terminal moraine northwards, and the southern karyotype ($2N = 46$) from the same point south. They suggest that the $2N = 52$ karyotype (*S. transitionalis*) arose sometime in

the late Wisconsinan and subsequently dispersed northwards with the development of oak-chestnut forests as the ice-shelf retreated. However, we propose that the splitting of the ancestral leporid by the Champlain-Hudson outflow is an equally likely hypothesis as to how these two species arose in allopatry. The $2N = 46$ karyotype was, as in this study, similarly regarded by Ruedas et al. (1989) as being largely restricted to animals from high elevation Appalachian habitat.

The proposed contact zone between two species is illustrated in Fig. 7 together with collection localities from this region which are incorporated in the present study. The Hudson River flows through a deep glacial cut in the area from Albany, New York south to the Atlantic Ocean and is subject to tidal influence. The area in, and around, Warren and Essex Counties, New York, is not characterized by a major river valley and movement between *Sylvilagus* sp. nov. and *S. transitionalis* could undoubtedly occur. Thus, we hypothesize that overlap of the two species has occurred in this region and it is likely that the two groups have moved down along both banks of the Hudson River sometime in the last 5,000–10,000 yr and this may represent a natural contact zone between them. Handley (1971:285) points out that there are numerous examples of “closely related pairs of species in the Appalachians” and that “most of them show some degree of competitive exclusion.”

Given our delineation of the two taxa (*S. transitionalis* north and northeast of the Hudson River; *Sylvilagus* sp. nov. strictly Appalachian in distribution), it is noteworthy that material referable to either species from the lower elevations and plains abutting the eastern reaches of the Appalachian mountains and eastward to the Eastern Seaboard, appears absent from current museum collections. While this may merely reflect a sampling bias, it is also possible that competition with the eastern cottontail, *S. floridanus*, may have hampered the expan-

sion of both species into these areas and the two in fact, may be absent from this region (Handley 1971, Chapman & Morgan 1973, Chapman & Fuller 1975).

Habitat

The description of the habitat of *S. transitionalis* reported by Chapman & Stauffer (1981) included the geographic range of the new cottontail. Consequently, we attempt to more accurately define habitat preferences of both species. Several detailed habitat studies of *S. transitionalis* in New England (the range of *S. transitionalis* s. s.), have been published (Fay & Chandler 1955, Nugent 1968, Linkkila 1971, Johnston 1972, Jackson 1973). These authors found no clear relationship of *S. transitionalis* to any forest region or land use as was detailed by Johnston (1972) for the species in southern New England. Jackson (1973) reported declining New England cottontail populations and believed the decline resulted from habitat change associated with older forest types. He indicated that the species was commonly associated with pines (*Pinus* spp.), grasses, hardwoods (general), birches (*Betula* spp.), oaks (*Quercus* spp.), blackberry and raspberry (*Rubus* spp.), panicled dogwood (*Cornus racemosa*), alders (*Alnus* spp.), common juniper (*Juniperus communis*), sugar maple (*Acer saccharum*), nursery plantings, cherries (*Prunus* spp.), goldenrod (*Solidago* spp.), sweetfern (*Comptonia peregrina*), staghorn sumac (*Rhus typhina*), maple-leafed viburnum (*Viburnum acerifolium*), bracken fern (*Pteridium aquilinum*), asters (*Aster* spp.), high-bush blueberry (*Vaccinium corymbosum*), hawthorn (*Crataegus* spp.), apple (*Pyrus malus*), and mosses (Jackson 1973, Table 3). Furthermore, the species has been recorded in virtually all habitat types in southern Connecticut (Nugent 1968).

In contrast, the Appalachian cottontail is strictly associated with dense cover and conifers at higher elevations along the Appalachian mountain chain (Llewellyn & Han-

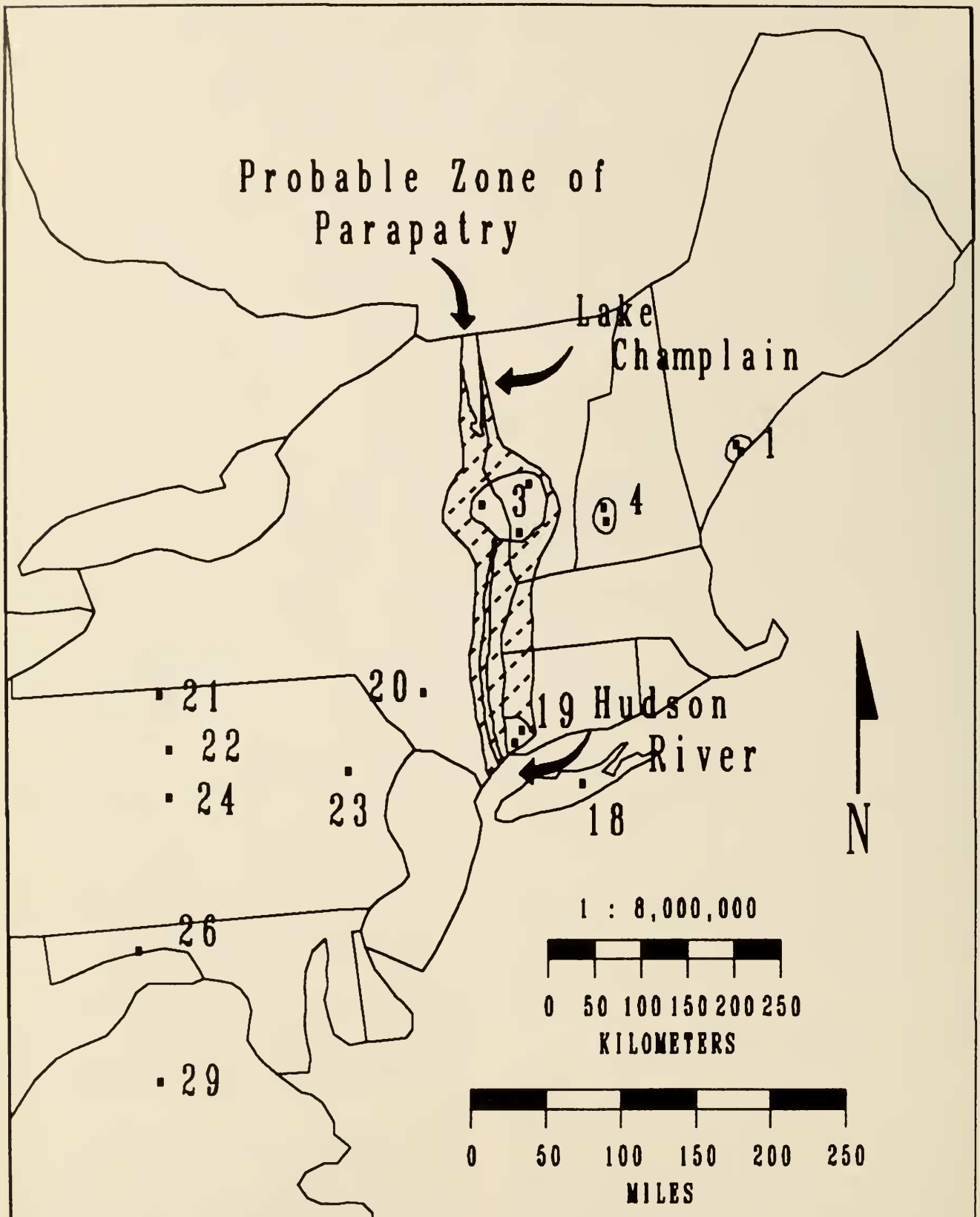


Fig. 7. Detailed map of the likely zone of parapatry between *S. transitionalis* and *S. obscurus*. See Table 1 and Gazetteer for populations comprising each geographic OTU.



Fig. 8. Photograph of the type locality of the Appalachian cottontail, *S. obscurus*, at the Dolly Sods Scenic Area, Grant Co., West Virginia.

dley 1945, Chapman & Stauffer 1981, Fig. 8). In Maryland, West Virginia, Georgia and Alabama the species is associated with conifers and heath habitat, especially *Kalmia* and *Vaccinium*, both characteristic species of high elevation or boreal environments (Chapman & Morgan 1973, Chapman & Stauffer 1981). In Virginia, the Appalachian cottontail occurs within 6–7 year old clear-cuts in the higher elevations (Blymyer 1976). Howell (1921) reported the species on mountain slopes and associated foothills in Alabama. Chapman & Morgan (1973:11–12) described the habitat of the Appalachian cottontail type locality (Fig. 8) in detail as: “a high wind-swept plateau along the Allegheny Front in northern West Virginia. The exposed bedrock reaches to over 1100 m in elevation. The area abounds with small ponds and streams. Most of the vegetation has suffered mechanical damage

from winterkill and the persistent, strong winds from the west. Originally, the area was completely covered with a climax forest of red spruce (*P. rubens*). The entire area was denuded of trees by heavy logging and subsequent fires in the late 1800’s. The forest destruction resulted in the existence of large areas of heath and scrubby trees maintained by periodic fires. The heath plains and bogs host rhododendron, mountain laurel, blueberry *Vaccinium corymbosum*, arbutus *Epigaea repens*, winterberry *Ilex verticillata*, deerberry *V. stamineum*, and cranberry *V. oxycoccus*. Throughout the heath, red spruce, hemlock, and pines grow singly or in groups. Forested areas bordering the heath plains consisted mainly of yellow birch, beech, fire cherry (*P. pennsylvanica*), red maple, striped maple, serviceberry (*Amelanchier humilis*), mountain ash (*P. americana*), mountain holly (*I. montana*),

aspens (*Populus* spp.) and hawthorn. The New England [=Appalachian] cottontail predominates on the plateau and is abundant in the heather and low scrub." From these accounts it is clearly apparent that the Appalachian species is associated with conifers and ericaceous vegetation characteristic of high altitude or boreal habitats.

Species Descriptions

Sylvilagus transitionalis (Bangs, 1895) New England Cottontail

Lepus sylvaticus transitionalis, Bangs, 1895: 405.

Sylvilagus transitionalis, Nelson 1909:195.

Holotype.—MCZ B 2407 adult, male, skin and skull, from Liberty Hill, New London Co., Connecticut. Collected 6 Nov 1894 by O. Bangs. (See remarks.)

Topotypes.—MCZ B 1206 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 1207 adult, female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2408, adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2409, adult, female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2410 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 2411 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5613 female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5635 adult, male, skull, Liberty Hill, New London Co., Connecticut. MCZ B 5635 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5640 adult, female, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5641 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut. MCZ B 5642 adult, male, skin and skull, Liberty Hill, New London Co., Connecticut.

Range.—Previously widely distributed in

New England north to Rutland, Vermont, southern New Hampshire, extreme southwestern Maine, southwest through eastern New York (Nelson 1909) to the eastern bank of the Hudson River. Currently restricted to boreal habitat in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island and in New York as far west as the Hudson River (Fig. 9).

Diagnosis.—Medium-sized cottontail with dorsal parts pinkish buff to ochraceous buff, overlain with black hairs giving the species a lined effect. There is a distinct black edge on the ears and usually a distinct black spot between the ears. The postorbital process is thin and tapering and the supraorbital process is lacking or jagged or irregular in outline (Chapman 1975).

Remarks.—Bangs (1895:408) lists the type of *S. transitionalis* No. 2407 as an adult female; however, the skin and skull are both identified as a male. Topotype B2409 is an adult female not a male. B 11 was collected in 1893. B 1800 was exchanged to E.R. Warner in 1910. The distribution of *S. transitionalis* as herein described is much reduced from that previously reported (Nelson 1909, Chapman & Morgan 1973, Chapman 1975, Chapman & Stauffer 1981, Chapman et al. 1982, Chapman & Ceballos 1990). There has not been a population of *S. transitionalis* at the type locality for some time (Johnston 1972). O. Bangs designated the series of topotypes listed above which would appear to represent the paratypes for *S. transitionalis*.

Specimens examined.—Holotype, topotypes, and 173 specimens from localities listed below. The numbers following county names refer to numbers of specimens examined from each locality.

Maine: Cape Elizabeth, Cumberland Co., 2 (USNM); Gray, Cumberland Co., 1 (USNM).

New Hampshire: Enfield, Grafton Co., 1 (USNM); West Lebanon, Grafton Co., 1 (UM); Newport, Sullivan Co., 1 (USNM);



Fig. 9. Current distribution of *S. transitionalis*. Distribution map based on this study and data collected by Chapman and Stauffer (1981).

Lempster, Sullivan Co., 1 (USNM); Concord, Merrimack Co., 1 (USNM); Bow, Merrimack Co., 1 (USNM); Swanzey, Cheshire Co., 2 (USNM); Rindge, Cheshire Co., 1 (USNM); Walpole, Cheshire Co., 1 (USNM); Cold River, Cheshire Co., 1 (USNM); Nashua, Hillsborough Co., 2 (USNM); Hancock, Hillsborough Co., 1 (USNM); Manchester, Hillsborough Co., 1 (USNM); Greenville, Hillsborough Co., 1 (USNM); Litchfield, Hillsborough Co., 1 (USNM); Milford, Hillsborough Co., 1 (USNM); Somersworth, Strafford Co., 1 (USNM); Durham, Strafford Co., 1 (USNM); Windham, Rockingham Co., 1

(USNM); Greenland, Rockingham Co. 1 (UM).

Vermont: Dorset, Bennington Co., 1 (USNM); Mendon, Rutland Co., 1 (USNM); Vernon, Windham Co., 2 (USNM); Saxtons River, Windham Co., 1 (CFM).

Rhode Island: Charleston, Providence Co., 1 (USNM); Wallum Lake, Providence Co., 1 (USNM); Worden Pond, Washington Co., 1 (USNM); Exeter, Washington Co., 7 (USNM); Richmond, Washington Co., 5 (USNM); North Kingston, Washington Co., 6 (USNM); Wolf Rock, Washington Co., 1 (USNM); Arcadia, Washington Co., 1 (USNM); Middlebridge, Washington Co., 1

(USNM); Pettasquamsutt, Washington Co., 1 (USNM); Washington Co., 4 (USNM).

Massachusetts: Rowe, Franklin Co., 2 (USNM); Birch Hill, Worcester Co., 6 (USNM); Royalston, Worcester Co., 1 (USNM); Wilmington, Middlesex Co., 11 (USNM); Dunstable, Middlesex Co., 2 (USNM); Shirley, Middlesex Co., 1 (USNM).

Connecticut: Barn Island, New London Co., 7 (USNM); Waterford, New London Co., 2 (USNM); Pawcatuck, New London Co., 1 (PM); Niantic, New London Co., 2 (PM); Franklin, New London Co., 1 (USNM); Salem, New London Co., 1 (USNM); Norwich, New London Co., 1 (USNM); Plainfield, New London Co., 2 (USNM); Stonington, New London Co., 1 (USNM); Ashford, Windham Co., 2 (USNM); Pomfret-Abington, Windham Co., 1 (USNM); Sterling, Windham Co., 3 (USNM); Windham, Windham Co., 1 (USNM); Warrenville, Windham Co., 3 (USNM); Thomson, Windham Co., 3 (USNM); Woodstock, Windham Co., 1 (USNM); Westford, Windham Co., 4 (USNM); Lebanon, Windham Co., 1 (USNM); Chaplin, Windham Co., 1 (USNM); Killingly, Windham Co., 1 (USNM); Mansfield, Tolland Co., 2 (USNM), 1 (PM); Storrs, Tolland Co., 9 (USNM); Stafford Springs, Tolland Co., 4 (USNM); Amston-Hebron, Tolland Co., 1 (USNM); Horsebarn Hill, Storrs, Tolland Co., 2 (USNM); Willington, Tolland Co., 1 (USNM); Westbrook, Middlesex Co., 1 (AM); East Haddam, Middlesex Co., 1 (USNM); Killingsworth, Middlesex Co., 1 (USNM); North Granby, Hartford Co., 1 (USNM); New Haven, New Haven Co., 1 (PM); Southbury, New Haven Co., 2 (USNM); Milford, New Haven Co., 1 (PM); Sharon Mountain, Litchfield Co., 2 (AM); Macedonia Brook State Park, Litchfield Co., 1 (AM); Torrington, Litchfield Co., 2 (USNM); Cornwall, Litchfield Co., 1 (USNM); Canaan, Litchfield Co., 1 (USNM); Woodbury, Litchfield Co., 1

(USNM); Easton, Fairfield Co., 3 (USNM); Fairfield-Larsen WS, Fairfield Co., 3 (USNM); Fairfield, Fairfield Co., 3 (USNM); Danbury, Fairfield Co., 1 (USNM).

New York: Monticello, Sullivan Co., 1 (AM); Mastic, Suffolk Co., 3 (AM); Hastings, Westchester Co., 1 (AM); Sing-Sing, Westchester Co., 2 (USNM).

Sylvilagus obscurus, new species
Appalachian Cottontail
Fig. 10

Holotype.—USNM 567187, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia. Collected 8 Apr 1974 by Joseph A. Chapman. Field no. DS-58.

Allotype.—USNM 567189, male, skin and skull, from near Davis, Tucker Co., West Virginia. Collected 17 Aug 1974 by Joseph A. Chapman. Field No. DS-82.

Paratypes.—USNM 567195, adult, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-97. USNM 567186, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-46. USNM 567196, adult, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. CAZ 7. USNM 567185, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-45. USNM 567183, adult, female, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-28. USNM 567198, adult, male, skull, Route 93 near Tucker Co. line, Grant Co., West Virginia, Field no. DS-69. USNM 567184, adult, male, skin and skull, from Dolly Sods Scenic Area, Grant Co., West Virginia, Field no. DS-33. USNM 567197, adult, male, skull, from near Davis, Tucker Co., West Virginia, Field no. CAZ 11. USNM 567191, female, skin and skull, near Davis, Tucker Co., West Virginia, Field no. DS-86. USNM 567192, immature, female, skin and skull, near Davis, Tucker Co., West Virginia, Field no. DS-



Fig. 10. Photograph of the Appalachian cottontail, *Sylvilagus obscurus*, taken at Spruce Knob, West Virginia, near the type locality (elevation 1463 m). Photograph by Joseph A. Chapman.

88. USNM 567194, immature, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-94. USNM 567190, immature, female, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-83. USNM 567188, immature, female, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-77. USNM 567193, male, skin and skull, from near Davis, Tucker Co., West Virginia, Field no. DS-93.

Range.—Occurs only within the Appalachian Mountain chain, its marginal plateau and mountain balds from the Hudson River southwest through Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia and Alabama (Fig. 11). The rabbit is presently distributed in discrete populations in the higher elevations and balds in a pattern similar to that of a refugial relict (Chapman & Stauffer 1981). A detailed range map of the type locality and the surrounding areas is presented in Chapman et al. (1977).

Diagnosis.—Medium-sized rabbit, with fine, silky fur. The upper sides are pinkish buff to ochraceous buff in color while the venter is bright whitish to pale buffy whitish, fore legs are rusty rufous. The cheeks have a distinct gray-grizzled appearance. The ears are short and rounded with the anterior edges covered with an edging of distinct black hair. There is usually a distinct black spot between the ears, and rarely a prominent white spot or blaze on the forehead (one example USNM 567191). Skull is grossly similar in appearance to that of *S. transitionalis*.

Comparisons.—*S. obscurus* differs from *S. transitionalis* in that the adult skull (length 65.5–75.2 mm) is proportionately shorter anteriorly (as reflected in the hard palate: palate vacuity ratio) and narrower medially (as reflected in the I¹ breadth: anterior frontal breadth and hard palate: anterior frontal breadth ratios) (Table 5). Nelson (1909:198) noted that specimens of *S. transitionalis* [*S. obscurus*] “with the heaviest skulls exam-

ined are from Alexandria, Virginia, and Travelers Repose, West Virginia.”

The single specimen from Alexandria, Virginia, included in our preliminary investigations was found to behave inconsistently in both the univariate and multivariate analyses. This, coupled to its position well outside the ranges of either *S. transitionalis* or *S. obscurus*, as defined by this study, resulted in its exclusion from the 274 specimens comprising our final data set. The need for new material from this locality is clearly indicated both to ensure against incorrect species identification, as well as to determine possible relationship to other *Sylvilagus*. Additional sampling, especially in the New York area, is important to further delineate the distribution of these two species.

None of the pelage characteristics are clearly diagnostic for differentiating between *S. obscurus* and *S. transitionalis*. Furthermore, in the absence of cytogenetic data, which provides for the unequivocal identification of these sibling species, our data show that practical cranial delineation rests on the detection of subtle differences in the anterior and medial portions of the skull. Correct identification of specimens can be obtained using the results of the discriminant function analysis (see Table 3 for details).

Remarks.—The scientific name *S. obscurus* is given to this species because of its secretive and elusive behavior and its similar appearance to *S. transitionalis*. The common name Appalachian Cottontail refers to the distribution of the species which is wholly within the Appalachian Mountain chain. The type locality lies on the border between Grant and Tucker counties, West Virginia.

Specimens examined.—Holotype, allotype, paratypes and 86 specimens from localities listed below. The numbers following county names refer to the number of specimens examined from each locality.

Pennsylvania: Ulysses, Potter Co., 2 (CM);

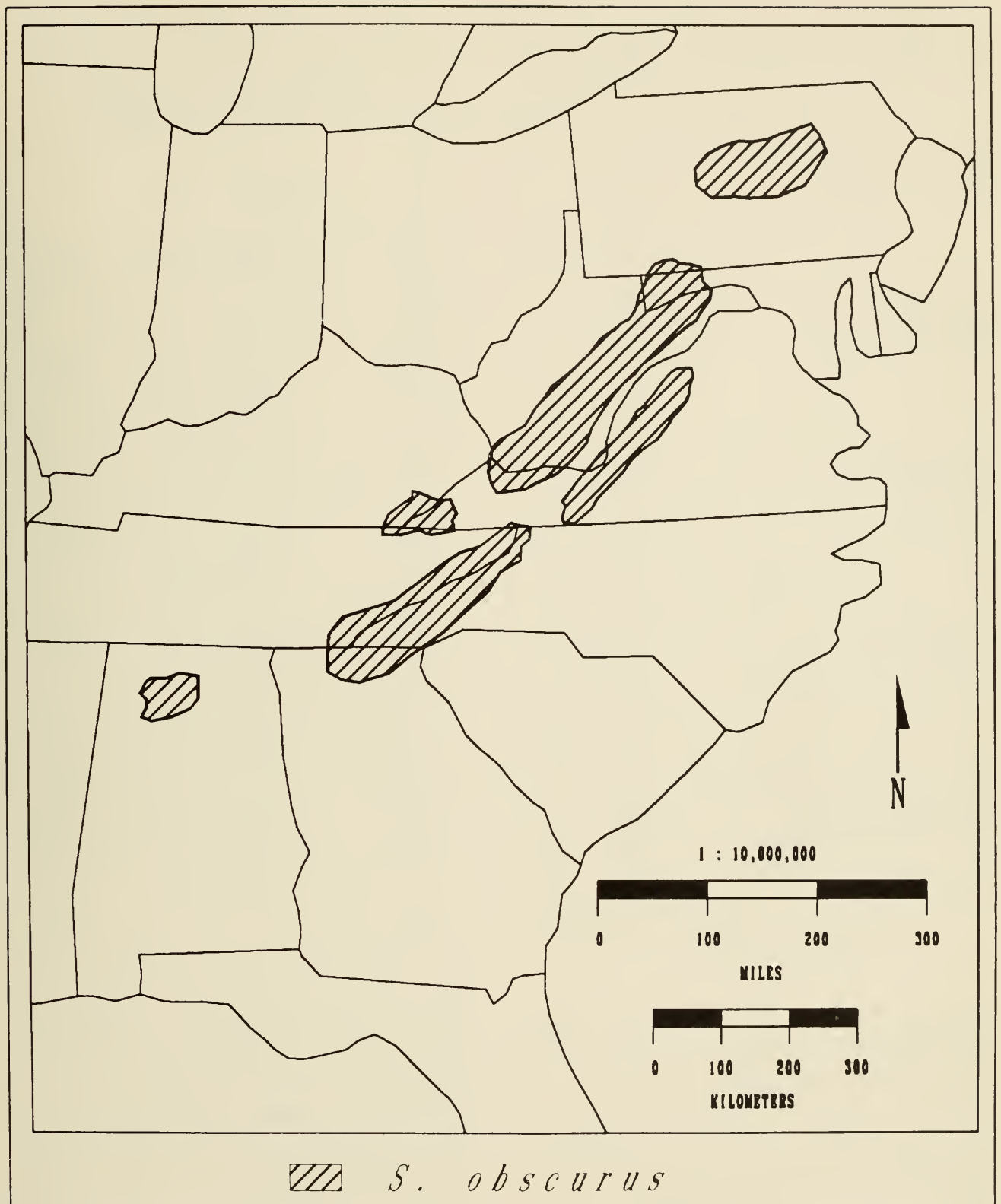


Fig. 11. Current distribution of *S. obscurus*. Distribution map based on this study and data collected by Chapman and Stauffer (1981).

Renovo, Clinton Co., 1 (USNM); White Haven, Luzerne Co., 1 (CM); Wingate, Centre Co., 1 (CM); Cashtown, Adams Co., 1 (CM); Powdermill Nature Preserve, West-

moreland Co., 1 (CM); Meyersdale, Somerset Co., 1 (CM); Markleysburg, Fayette Co., 1 (CM).
 Maryland: Warnick Point, Garrett Co., 2

Table 5.—Variation in ratios calculated by contrasting selected measurements with high positive and negative loadings on Principal component II. Standard deviations estimates were based on a single sample comprising large numbers of specimens; *S. transitionalis* (OTU 14, $n = 65$) and *S. obscurus* (OTU 28, $n = 28$).

Ratio	<i>S. transitionalis</i>		<i>S. obscurus</i>	
Hard palate length \times 100/ Palate vacuity length	Mean	35.82	Mean	32.70
	Max	43.04	Max	38.45
	Min	28.29	Min	27.58
	Mean + <i>SD</i>	38.46	Mean + <i>SD</i>	34.84
	Mean - <i>SD</i>	33.18	Mean - <i>SD</i>	30.56
	<i>n</i>	178.00	<i>n</i>	92.00
I ¹ breadth \times 100/ Palate vacuity length	Mean	15.89	Mean	14.86
	Max	17.83	Max	17.54
	Min	13.75	Min	12.80
	Mean + <i>SD</i>	16.59	Mean + <i>SD</i>	15.50
	Mean - <i>SD</i>	15.19	Mean - <i>SD</i>	14.22
	<i>n</i>	176.00	<i>n</i>	93.00
Hard palate length \times 100/ Parietal length	Mean	40.65	Mean	37.20
	Max	48.09	Max	44.61
	Min	32.78	Min	27.49
	Mean + <i>SD</i>	43.44	Mean + <i>SD</i>	39.82
	Mean - <i>SD</i>	37.87	Mean - <i>SD</i>	34.57
	<i>n</i>	175.00	<i>n</i>	89.00
I ¹ breadth \times 100/ Anterior frontal breadth	Mean	18.57	Mean	16.18
	Max	21.31	Max	19.44
	Min	15.93	Min	13.48
	Mean + <i>SD</i>	19.73	Mean + <i>SD</i>	17.05
	Mean - <i>SD</i>	17.42	Mean - <i>SD</i>	15.32
	<i>n</i>	174.00	<i>n</i>	92.00
Hard palate length \times 100/ Anterior frontal breadth	Mean	41.88	Mean	35.76
	Max	50.22	Max	46.09
	Min	31.14	Min	26.44
	Mean + <i>SD</i>	44.98	Mean + <i>SD</i>	38.24
	Mean - <i>SD</i>	38.79	Mean - <i>SD</i>	33.27
	<i>n</i>	176.00	<i>n</i>	91.00

(USNM); New Germany, Garrett Co., 5 (USNM); Elk Lick, Garrett Co., 6 (USNM); Savage River State Forest, Garrett Co., 2 (USNM); Popular Lick, Garrett Co., 7 (USNM); Meadow Mountain, Garrett Co., 1 (USNM); Finzel, Garrett Co., 1 (USNM); Garrett Co., 1 (USNM); Frostburg, Alleghany Co., 1 (USNM).

West Virginia: Cacapon Mountain, Morgan Co., 1 (USNM); Dolly Sods, Grant Co., 16 (USNM), 1 (NC); Mt. Storm, Grant Co., 1 (USNM); Stony River Bridge, Route 50, Grant Co., 1 (USNM); Davis, Tucker Co., 4 (USNM); White Sulphur Springs, Greenbriar Co., 1 (USNM), 1 (CFM).

Virginia: Shenandoah National Park,

Madison Co., 1 (USNM); Elliot Knob, Augusta Co., 2 (USNM); Newman's Run, Allegheny Mountains, Highland Co., 3 (USNM); Mountain Lake, Giles Co., 1 (CFM); Sinking Creek Mountain, Montgomery Co., 1 (USNM); Haysi, Dickenson Co., 1 (USNM); Saltville, Smyth Co., 3 (USNM); Russell Co., 1 (USNM).

North Carolina: Roan Mountain, Mitchell Co., 3 (USNM).

South Carolina: Walhalla, Oconee Co., 1 (USNM).

Tennessee: Carvers Gap, Carter Co., 1 (USNM); Smoky Mountain Low Gap, Cocke Co., 1 (USNM).

Georgia: Young Harris, Towns Co., 2

(USNM); Brasstown Bald, Union Co., 1 (USNM).

Alabama: Ardell, Cullman Co., 1 (USNM); Flannigan Creek, Lawrence Co., 1 (USNM).

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University (MCZ), and the Peabody Museum, Yale University (PM). Terri McFadden, Museum of Comparative Zoology, Harvard University made available the specimens of *S. transitionalis* in the Bangs collection which include, the holotype and topotypes. The field specimens utilized during this study are now in the collection of the National Museum of Natural History. Dr. Raymond Dueser, Department of Fisheries and Wildlife, College of Natural Resources, Utah State University, reviewed the manuscript and made many helpful suggestions. Dr. John Schmidt, Department of Geography and Earth Resources, College of Natural Resources, and Dr. James A. MacMahon, College of Science, Utah State University provided a sounding board for ideas about the biogeography and systematics of the rabbits, respectively. Aspects of this study were conducted while NJD was the recipient of a Transvaal Museum Research Associateship; this support is gratefully acknowledged. The Ecology Center, the office of the Vice President for Research, and the College of Natural Resources at Utah State University provided funding for the publication of this manuscript. Tom Van Neil and Nathan Bentley prepared the maps, and Cindy Howard, Penny Simmons and Pauline Davis typed the manuscript.

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Appendix I—Specimens Included in Analysis

The numbers preceding each locality can be used to determine the geographic grouping of OTUs in the multivariate analysis (See Table 1).

Maine: (1) Gray, Cumberland Co.; (2) Cape Elizabeth, Cumberland Co.;

New Hampshire: (3) Enfield, Grafton Co.; (4) West Lebanon, Grafton Co.; (5) Newport, Sullivan Co.; (6) Lempster, Sullivan Co.; (7) Concord, Merrimack Co.; (8) Bow, Merrimack Co.; (9) Swanzey, Cheshire Co.; (10) Rindge, Cheshire Co.; (11) Walpole, Cheshire Co.; (12) Cold River, Cheshire Co.; (13) Hancock, Hillsborough Co.; (14) Manchester, Hillsborough Co.; (15) Nashua, Hillsborough Co.; (16) Greenville, Hillsborough Co.; (17) Litchfield, Hillsborough Co.; (18) Milford, Hillsborough Co.; (19) Somersworth, Strafford Co.; (20) Durham, Strafford Co.; (21) Windham, Rockingham Co.; (22) Greenland, Rockingham Co.;

Vermont: (23) Dorset, Bennington Co.; (24) Mendon, Rutland Co.; (25) Vernon Windham Co.; (26) Saxtons River, Windham Co.;

Massachusetts: (27) Rowe, Franklin Co.; (28) Birch Hill, Worcester Co.; (29) Royalston, Worcester Co.; (30) Wilmington, Middlesex Co.; (31) Dunstable, Middlesex Co.; (32) Shirley, Middlesex, Co.;

Rhode Island: (33) Wallum Lake, Providence Co.; (34) Arcadia, Washington Co.; (35) Exeter, Washington Co.; (36) North Kingston, Washington Co.; (37) Pettaquamscutt, Washington Co.; (38) Charleston, Washington Co.; (39) Worden Pond, Washington Co.; (40) Wolf Rock, Washington Co.; (41) Middlebridge, Washington Co.; (42) Richmond, Washington Co.; (43) Washington Co.;

Connecticut: (44) Westbrook, Middlesex Co.; (45) East Haddam, Middlesex Co.; (46) Killingsworth, Mid-

dlex Co.; (47) Barn Island (Stonington), New London Co.; (48) Pawcatuck, New London Co.; (49) Niantic, New London Co.; (50) Ashford, Windham Co.; (51) Pomfret-Abington, Windham Co.; (52) Windham, Windham Co.; (53) Warrenville, Windham Co.; (54) Thomson, Windham Co.; (55) Putnam, Windham Co.; (56) Franklin, New London Co.; (57) Salem, New London Co.; (58) Woodstock, Windham Co.; (59) Lebanon, Windham Co.; (60) Mansfield, Tolland Co.; (61) Norwich, New London Co.; (62) Plainfield, New London Co.; (63) Chaplin, Windham Co.; (64) Westford, Windham Co.; (65) Sterling, Windham Co.; (66) Stonington, New London Co.; (67) Killingly, Windham Co.; (68) Storrs, Tolland Co.; (69) Waterford, New London Co.; (70) Stafford Springs, Tolland Co.; (71) Willington, Tolland Co.; (72) Amston-Hebron, Tolland Co.; (73) New Haven, New Haven Co.; (74) Milford, New Haven Co.; (75) Sharon Mountain, Litchfield Co.; (76) Macedonia Brook SP, Litchfield Co.; (77) Cornwall, Litchfield Co.; (78) Woodbury, Fairfield Co.; (79) Torrington, Litchfield Co.; (80) Canaan, Litchfield Co.; (81) Danbury, Fairfield Co.; (82) Fairfield, Fairfield Co.; (83) Fairfield, Larson Wildlife Sanctuary, Fairfield Co.; (84) Easton, Fairfield Co.; (85) North Granby, Hartford Co.; (86) Southbury, New Haven Co.;

New York: (87) Mastic, Suffolk Co.; (88) Hastings, Westchester Co.; (89) Sing-Sing, Westchester Co.; (90) Monticello, Sullivan Co.; (91) Lake George, Warren Co.;

Pennsylvania: (92) Ulysses, Potter Co.; (93) Renovo, Clinton Co.; (94) White Haven, Luzerne Co.; (95) Win-

gate, Centre Co.; (96) Cashtown, Adams Co.; (97) Powdermill Nature Preserve, Rector, Westmoreland Co.; (98) Meyersdale, Somerset Co.; (99) Markleysburg, Fayette Co.;

Maryland: (100) New Germany, Garrett Co.; (101) Hummel Farm, Garrett Co.; (102) Poplar Lick, Garrett Co.; (103) Elk Lick, Garrett Co.; (104) Savage River, Garrett Co.; (105) Meadow Mountain, Garrett Co.; (106) Frostburg, Garrett Co.; (107) Garrett Co.; (108) Warnick Point, Garrett Co.; (109) Finzel, Garrett Co.;

West Virginia: (110) Dolly Sods, Grant Co.; (111) Mount Storm, Grant Co.; (112) Stony River, Grant Co.; (113) Dolly Sods, Tucker Co.; (114) Davis, Tucker Co.; (115) Cacapon Mt, Morgan Co.; (116) White Sulphur Springs, Greenbrier Co.;

Virginia: (117) Shenandoah National Park, Madison Co.; (118) Elliot Knob, Augusta Co.; (119) Newman's Run, Allegheny Mountains, Highland Co.; (120) Mountain Lake, Giles Co.; (121) Sinking Creek Mountain, Montgomery Co.; (122) Haysi, Dickenson Co.; (123) Saltville, Smyth Co.; (124) Russell Co.;

Tennessee: (125) Smoky Mountain Low Gap, Cocke Co.; (126) Carvers Gap, Carter Co.;

North Carolina: (127) Roan Mountain, Mitchell Co.;

South Carolina: (128) Walhalla, Oconee Co.;

Alabama: (129) Flannigan Creek, Black Warrior Wildlife Management Area, Lawrence Co.; (130) Ardell, Cullman Co.;

Georgia: (131) Young Harris, Towns Co.; (132) Brasstown Bald, Towns Co.;